Planema eschria to D. All of them were eaten, though

D seemed a little suspicious at first.

19. Gave Byblia goetzius-acheloia to  $\Lambda$ , which ate it readily, although she was a long time before coming down to see what it was.

20. Gave wingless specimens of Λ. horta to spiders A, B, C, and D (six days since last were given—Experiment 16). The first three promptly ejected them, but D wrapped hers up and carried it off. She did not seem very enthusiastic about it however, for she turned it over and over a good many times, giving it a bite here and there, and then left it alone for some time. This procedure she repeated several times, and then threw it away.

21. Gave entire males of Acrea serena-buxtoni to spiders A, C, and D, all of which were eaten. It should be noted that experiments with this species are unsatisfactory, owing to the fact that when captured it is able voluntarily to exude from the thorax its bitter yellow juice, and therefore when given to spiders it has lost much of its nauseous quality, and would be less distasteful than if caught by them direct.

5. Results of Experiments on Spiders and the earlier Experiments on Mantidæ: One probable meaning of tenacity of Life in distasteful Insects. (G. A. K. M.)

Malvern, Natal; February 21, 1897.—The danger of arguing from insufficient materials was clearly shown me in my first few experiments on spiders with A. horta (Experiments 1, 2, 3, and 6). When I had got thus far I felt sure I had got proofs of the appreciation of warning colours by the spiders. For in these experiments they ate every specimen without wings and refused all those with them except one which had the colour rubbed off. Yet subsequent experiments have convinced me that both spiders and Mantises have no appreciation of warning colours; and this fact has elucidated another which often puzzled me, I mean the apparently constant correlation between distastefulness and tenacity of life in Lepidoptera. At first sight it would seem that tenacity of life or the power to recover after severe injury would be useful to any species in the struggle for existence. But a little thought showed me that this power would be of no use to edible species, as if once eaught by insectivorous animals

they are not likely to be released. But in the case of inedible species it is different. For if my surmise is true, that insectivorous invertebrates are not capable of appreciating warning colours but have to taste all their captives before being able to tell whether they are edible or not (which I think is clear from my experiments), then tenacity of life (as a protective agency) will be as useful an acquisition against invertebrates as warning coloration is against vertebrates, and come into play when the latter is useless. Of course tenacity is of use against the experimental tasting of young birds, lizards etc., but this does not seem to me to be a sufficiently cogent factor to develop the power to such a high pitch. For if the insects had only these enemies to contend against, even supposing every specimen experimentally tasted died from its injuries, the protection afforded by the warning colours would still be ample. Indeed I believe that the toughness of inedible insects has been primarily developed to counteract the injuries from invertebrate foes (which are incapable of reasoning as to whether an insect is edible or not), and that therein lies its chief utility, though it may prove useful incidentally in other cases.

A. buxtoni appears to have more juice in proportion than horta, and I regard it as a more highly-developed species, from a distasteful point of view, in that it can exude juice at will from its thorax, and thus show its nauseous qualities without necessarily having to be injured like horta. When squeezed the juice often oozes from the ends of the antennæ and all the nervures of the fore-wings when they are cut. But, as I have pointed out (vide Expt. 21), the results of experiments with it

are unreliable.

The treatment of A. horta by the spiders would almost give some colour to your suggestion that the inedibility of species may be due to unpleasant internal effects rather than the mere taste, for B ate one specimen and A, C, and D two each before they seemed to become aware that it was not good to eat, from which I should conclude either that the unpleasant effects are subsequent to eating or that their sense of taste is not sufficiently acute to recognize a nasty flavour at once. But the latter conclusion appears to be invalidated by their prompt rejection of L. chrysippus and A. echeria. Anyway their selection seems to show that there are grades of unpleasantness, and, as I

expected, those species in which the sexes are alike are least edible. Thus I expect to find that A. uncmosa, A. cabira, and P. aganice will prove more distasteful than their allies in which the sexes differ markedly. However, I must admit that in the case of the Mantis this was not so, and its persistent preference for echeria rather than horta (on three occasions) is very curious and interesting. Its dislike of the taste of horta was most marked, and yet it did not appear to distinguish it by sight. In Experiment II. e(p. 298) the Mantis certainly avoided horta after its first taste, but it showed equal fear of echeria, which it afterwards ate, and I presume could not distinguish between them. But it is clear that it was unable to retain long the impression which connected a butterfly with an unpleasant taste. The prompt acceptance of A. serena by the spiders appears to support my view that the bright red colour conveys no significance to them, although they find the red horta distasteful. I was surprised at their unanimous refusal of the single specimen of A. violarum I was able to procure, as I had thought it would certainly be more edible than horta, and I am almost inclined to believe that it was rejected under a misapprehension.

I had an idea that perhaps Papilio demodocus was distasteful, which was suggested by its wide range and general abundance; and that if this were so it would be probable P. ophidicephalus, P. cuphranor, P. constantinus, etc., might obtain protection from their strong resemblance to it on the wing. But my experiments seem to negative the

idea as far as invertebrate foes are concerned.

Again, Terius has always puzzled me. They are so widely distributed and always plentiful; moreover, their flight is weak and their contrasting colours of black and yellow are most conspicuous on the open veldt, which they frequent; indeed, far more so than the colours of the females of A. violarum and noharu. Yet they do not seem to be protected, although some of the tropical Durbanias and Teriomimae appear to minic them.

Malvern, Natal; Oct. 7, 1897.—The experiments on the effects of an Acraa diet, so far as they go, seem to lend some measure of support to your view as to the unwholesome qualities of Acraa, though many more experiments will be necessary to establish it. If I could only get the material I should like to experiment contemporaneously on a number of the same species, starving one, giving one or two only edible butterflies, and confining the remainder to a single species of Acrea or Amauris each. But at present I find it not only difficult to get hold of a Mantis, but it is even quite a job to catch sufficient Acreas to continue the experiments. I have not seen a single specimen of A. petraa for over six weeks, though normally it should be swarming at this time of year.

[Mr. Marshall subsequently carried out a part of the programme which he here suggests. See Experiments

IX., X., XI. on Mantida.]

When the experiments on spiders are compared with those on Mantises the conclusion is suggested that Acraina were distasteful to both, and only eaten under the stress of hunger, while Danaina were far less distasteful to the Mantises than to the spiders. To the latter they appeared to be at least as distasteful as the Acraina. Such differences in the susceptibilities of insect-eaters help us to understand the puzzling case of Terias, and the Ethiopian Lycaenid genera which appear undoubtedly to mimic it, and permit us still to look on Papilio demodocus as a possible model. We see that the various insectivorous groups have different tastes, and within each group we must expect to find individual species adapted to feed largely on insects which are as a rule rejected by the other members of the same group.

In one respect spiders are extremely satisfactory for the purpose of these experiments. They remain throughout wild animals with their natural sources of food still available. The same may be the case with Mantides, as in the *Gongylus* watched day after day by Col. Yerbury at

Trinkomali (see p. 316).

The late Thomas Belt ("Naturalist in Nicaragua," London, 1888, p. 317) states that a "spider that frequented flowers seemed to be fond of" the *Heliconidæ* (including *Ithomiinæ*), although a large species of *Nephila* used to drop them out of its web when he put them into it.

Dr. A. G. Butler (Trans. Ent. Soc. Lond., 1869, p. 27) long ago showed that the larvæ of Abraxas yrossulariata and Halia wavaria were not eaten by the spiders he employed —Epeira diadema (the name given in the paper is Ereiba diadema) and Lycosa species (?). In the former case they were cut out of the web, and in the latter seized and carried down the "dark silken funnel," but then relinquished apparently uninjured. Professor Plateau (Mém.

de la Soc. Zool. de France, tome vii, 1894, p. 375) gives reasons for doubting whether the latter spider belonged to the genus named by Dr. Butler, and he supposes from the described form of "funnel" that the "Lycosa," which does not make a web, was in reality Agelena labyrinthica. Professor Plateau's fresh experiments (l. c. § 8) on spiders, however, entirely confirm the results obtained by Dr. Butler so far as the larva of Abraxas is concerned. An Amaurobius ferox, which had spun a characteristic web in captivity, paid no attention during two days to three half-grown larve moving about and entangled in the web. From the Professor's long experience of spiders in captivity he is confident that it was not afraid, and he thinks it probable that it refrained from attack because the vibration of the web was not like that caused by its habitual prey. It would have been more satisfactory if this interpretation had been tested by the offer of a few inconspicuous larvae. In the next experiment four larvæ were thrown into a large web spun by a female Tegenaria domestica over the roof-light of a barn in such a position that the observer could watch everything without in the least disturbing the spider. The following is a translation of Professor Plateau's account:—" At the moment of the fall of the larvæ into the web, the Tegenaria . . . . rushes at one of them and bites it, or at least makes two successive attempts to bite it. The spider then leaves the first victim and attacks a second, which she also tries to bite, but the skin of the larvæ being too tough and the caterpillars rolled up and pretending to be dead, she retires slowly, a certain proof to those who know the habits of these animals that she does not feel any fear." Afterwards, when the caterpillar began to move the web, the spider, "having learnt the uselessness of her attempts to bite, neglects them entirely and remains in her tube.

Concerning this and the previous interpretation, it is necessary to remark that no signs of fear were to be expected upon the hypothesis that the spider recognized that the larva was uneatable; while the suggestion that the skin was too tough to be penetrated seems to be very

improbable.

An experiment of the same kind was then made with a female *Tegenaria*, which spun a web in confinement. After keeping the spider for three days without food, two caterpillars were thrown into the web. The spider rushed

towards one of them but retreated again, "recognizing that it had been disturbed by a creature such as had never before fallen into the web." The same thing was again repeated on four occasions, the spider never actually attacking a caterpillar. Agelena labyrinthica was then tried in the same way, but would not leave its retreat; when, however, an earwig was substituted for the larva, it was instantly seized and devoured.

On the other hand, Professor Plateau has produced evidence that the imago of the *Abraxas* is freely eaten by *Tegenaria domestica*. Nearly every day for some weeks he placed this moth, sometimes on one, sometimes on another of three or four webs of this spider spun in a little tool-house in his garden. They were always seized and

carried off.

Agelena labyrinthica, on the other hand, killed the moth but abandoned it after some attempts to suck its juices. Professor Plateau suggests that the spider found the prey too large for it, an interpretation which might have been advanced had the attempt to capture and kill been unsuccessful; but, as the case stands, serves to show that the author is willing to accept any explanation however improbable rather than the obvious one that there was something in the taste or smell of the moth which prevented the spider from devouring it.

A half-grown female *Epeira diadema* devoured the moth with avidity. It is to be hoped that this experiment will be repeated many times, as in the case of the *Tegenaria*; and in all such researches comparison should be constantly made with the behaviour of the spiders towards many other

kinds of insects.

It is quite probable from the experiments of Mr. Marshall and Professor Plateau, and the observations of the late Mr. T. Belt, that certain species of spiders, together with Mantides and other predaceous insects, will be found to be among the chief, perhaps the chief, non-parasitic enemies of aposematic insects.

Colonel J. W. Yerbury has kindly searched his notes for any references to the attacks of spiders on butterflies. He writes, "I can find very few references to the relations of these two animals to each other in my old notes. The

following are two of them:—

"'Aden, ? date.—A large green flower-haunting spider resting on a dried-up plant was preying on a female

Teracolus vi. The specimen was almost the first female of the species which I obtained. The individuals of this butterfly roosted regularly on the stalks of the plant in question, their under-sides being of about the same tint as the dried-up leaves and stems.

"'Futchpore Sikri, near Agra, May 1877.—Spiders lay in wait for the Pierine Belenois mesentina, on the flowers of a caper (Capparis aphylla). On this occasion the spiders

took a very heavy toll of the butterflies." \*

[Mr. C. J. M. Gordon has sent to the Hope Department a male specimen of Acrau bonasia, which he found on January 8, 1902, at Old Calabar, in the grasp of a flower-haunting spider (Thomisus, sp.). The falces of the arachmid were fixed in the butterfly's thorax, and the insect was nearly dead.—E. B. P.]

6. The Attacks of Predaceous Insects other than Mantidle upon conspicuous specially-defended Lepidoptera, etc. (E. B. P.)

H. W. Bates, in the historic paper which contained the first suggestion of the theory of Protective Mimicry (Trans. Linn. Soc., vol. xxiii, 1862, p. 495), states concerning the attacks of predaceous insects: "I never saw the flocks of slow-flying Heliconidæ [in the writings of Bates and Belt upon Mimicry, the Heliconidæ always include the Ithominæ or Neotropinæ, then called the Danaoid Heliconidæ] in the woods persecuted by birds or Dragonflies, to which they would have been an easy prey; nor, when at rest on leaves, did they appear to be molested by Lizards or the predaceous Flies of the family Asilidæ, which were very often seen pouncing on Butterflies of other families" (p. 510).

There is, however, good reason for believing that such attacks are not rarely made, and that predaceous insects

are important enemies of aposematic butterflies.

In the following three sub-sections of this paper I have brought together some slight evidence in support of this conclusion. Far more requires to be done, and it is hoped that the attention which is here directed to the inquiry

<sup>\*</sup> Shortly after I had made the observation I came across a reference to this habit of the spiders at the very same place, but I cannot now recall the name of the publication.—J. W. Y.